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The Influence of Light and Temperature on Isoprene Emission Rates from Live Oak

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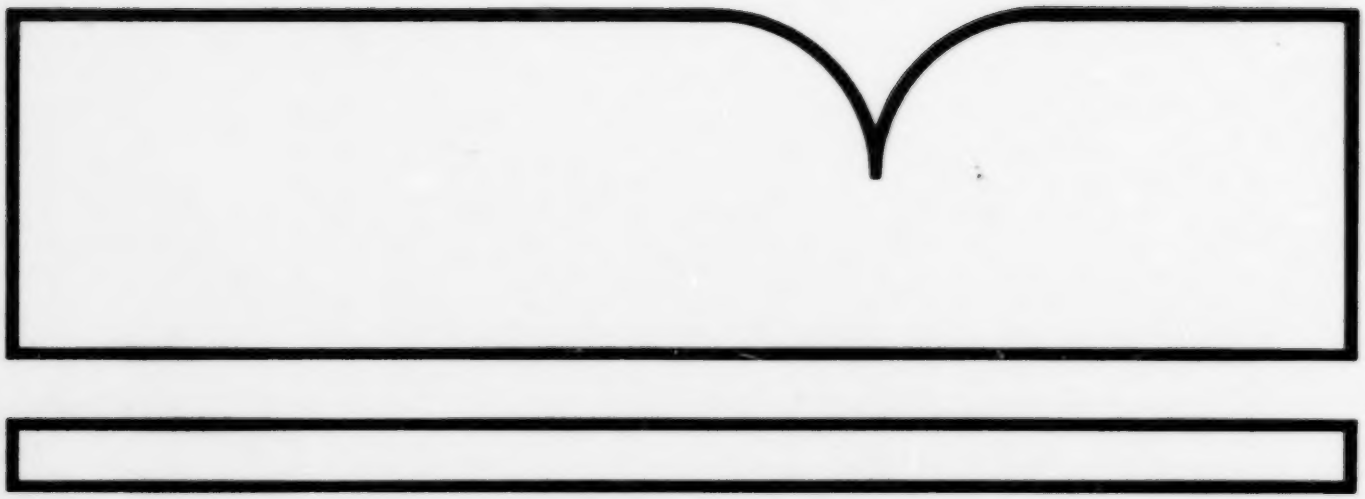

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16 ABSTRACT

There is a growing awareness of the role of vegetation as a source of reactive hydrocarbons that may serve as photochemical oxidant precursors. A study was designed to assess independently the influence of variable light and temperature on isoprene emissions from live oak (Quercus virginiana Mill.). Plants were conditioned in a growth chamber and then transferred to an environmentally controlled gas-exchange chamber. Samples of the chamber atmosphere were collected; isoprene was concentrated cryogenically and measured by gas chromatography. A logistic functions was used to model isoprene emission rates. Under regimes of low temperature (20°C) or darkness, isoprene emissions were lowest. With increasing temperature or light intensity, the rates of isoprene emission increased, reaching maxima at 800 $\mu E\ m^{-2}\ s^{-1}$ and 40-44°C, respectively. Higher temperatures caused a large decrease in emissions. Since the emissions of isoprene were light-saturated at moderate intensities, temperature appeared to be the main factor controlling emissions during most of the day. Carbon lost through isoprene emissions accounted for 0.1 to 2% of the carbon fixed during photosynthesis depending on light intensity and temperature.

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The Influence of Light and Temperature on Isoprene Emission Rates from Live Oak

By

DAVID T. TINGEY, MARYBETH MANNING, LOUIS C. GROTHAUS and WALTER F. BURNS

U.S. Environmental Protection Agency and Northrop Services, Inc., 200 S.W. 35th Street, Corvallis, Oregon 97330

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Abstract

There is a growing awareness of the role of vegetation as a source of reactive hydrocarbons that may serve as photochemical oxidant precursors. A study was designed to assess independently the influence of variable light and temperature on isoprene emissions from live oak (*Quercus virginiana* Mill.). Plants were conditioned in a growth chamber and then transferred to an environmentally controlled gas-exchange chamber. Samples of the chamber atmosphere were collected; isoprene was concentrated cryogenically and measured by gas chromatography. A logistic function was used to model isoprene emission rates. Under regimes of low temperature (20°C) or darkness, isoprene emissions were lowest. With increasing temperature or light intensity, the rate of isoprene emission increased, reaching maxima at 800 μE m^{-2} s^{-1} and 40–44°C, respectively. Higher temperatures caused a large decrease in emissions. Since the emissions of isoprene were light-saturated at moderate intensities, temperature appeared to be the main factor controlling emissions during most of the day. Carbon lost through isoprene emissions accounted for 0.1 to 2% of the carbon fixed during photosynthesis depending on light intensity and temperature.

Key words: *Quercus virginiana* — isoprene — hydrocarbon emission.

Introduction

High levels of ozone have been measured in urban, rural and remote areas far from significant anthropogenic sources of oxidant precursors. These elevated oxidant concentrations in remote and rural areas could result from transport into these areas and/or the photo-oxidation of locally produced biogenic hydrocarbons. It is unclear which process is more important, partly because biogenic emission rates of reactive hydrocarbons are not well known.

Isoprene (2-methyl-1,3-butadiene) has been identified as a volatile emission product from a wide range of plant species (*e.g.*, Rasmussen 1970, Sanadze and Kursanov 1966). The biogenic production of isoprene is light dependent (Rasmussen and Jones 1973, Sanadze and Kalandadze 1966b, Sanadze and Kursanov 1966) and increases with light intensity until the processes controlling emission are light saturated (Sanadze and Kaladadze 1966a). The action spectra of isoprene production exhibits a maximum in the red wave lengths (Rasmussen and Jones 1973, Sanadze and Kalandadze 1966b). The temperature coefficient (Q_{10}) of isoprene production varied between 2.8 and 3.6; emissions increased with temperature reaching a maximum between 35 and 43°C and decreased sharply at temperatures above 40 to 43°C (Sanadze and Kalandadze 1966a, Rasmussen and Jones 1973). Isotopically labeled CO_2 is incorporated readily into isoprene (Sanadze *et al.* 1972). The molecular distribution of the labeled carbon and studies with metabolic inhibitors suggest that glycolate and acetyl-CoA are metabolic intermediates in its biosynthesis (Jones and Rasmussen 1975, Sanadze *et al.* 1976).

Previous studies of isoprene emissions used either detached stems, leaves or leaf discs and/or expressed emissions in arbitrary units (*e.g.*, Sanadze and Kalandadze 1966a,b, Rasmussen and Jones 1973). The objectives of our study were (1) to determine isoprene emission rates from intact plants under carefully controlled environmental conditions, (2) to determine the independent influence of light and temperature on emission rates, and (3) to determine the relationship between isoprene emission rates and photosynthetic rates.

Methods and Materials

Plant culture. Live oak (*Quercus virginiana* Mill.) plants were obtained from the Division of Forestry, Florida Department of Agriculture and Consumer Services as seedlings and potted in 15-cm pots in a growth medium of Jiffy-mix: perlite (1:2; v:v) mixture. The oak plants were cultured in a greenhouse at maximum day/night temperatures of 23 and 18°C, respectively. Sunlight was supplemented and the photoperiod extended to 16 h/day with light from high intensity discharge sodium vapor lamps. The plants received half-

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strength modified Hoagland's nutrient (Downs and Hellmers 1975) solution daily. At least 4 weeks before sampling, oak plants were placed in a growth chamber and conditioned at maximum day/night temperatures of 27 and 18°C, respectively, with a 16-h photoperiod at a light intensity of 400 μE m^{-2} s^{-1}. The light was provided by both cool-white fluorescent (3800 watts) and incandescent (670 watts) lamps. Experimentation was conducted when the plants had both mature and young expanding leaves.

Gas-exchange chamber. A gas-exchange chamber similar conceptually to the one described by Huang *et al.* (1975) and exhibiting the mixing characteristics of a constant-stirred-tank reactor (Rogers *et al.* 1977) was used to determine isoprene emission rates (Figure 1). The gas exchange chamber was designed for use in a controlled environment chamber which regulated light and cooling. The two compartment design of the gas-exchange chamber permitted the independent control and monitoring of plant leaf and pot-root mass in the upper and lower compartments, respectively. To insert the plant, the upper chamber was removed and the pot-root mass was placed into the lower chamber. Two halves of the 24 cm. diam. disc with center cut out were fitted around the stem, set in place and sealed to the stem and chamber with modeling clay. The upper chamber was placed over the plant without injuring the leaves and sealed to the chamber base. Both upper and lower chambers contained fans with exterior motors and the upper chamber contained three 2.5 cm high baffles arranged equidistant around the walls of the chamber to promote mixing.

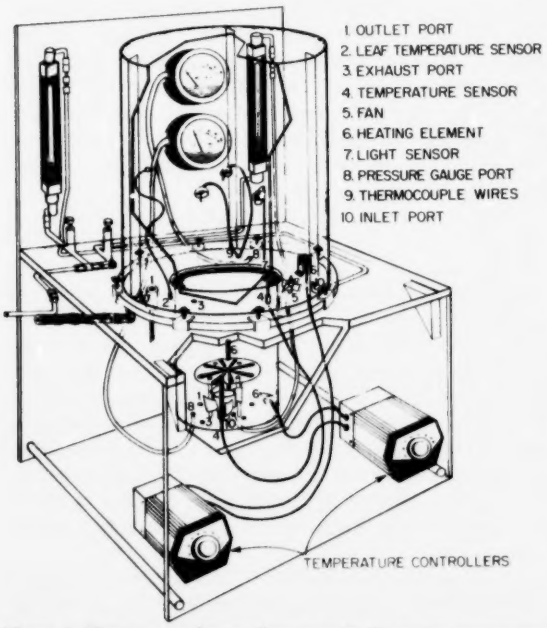

Figure 1. *Plant gas-exchange chamber with the major components identified.* The volume of the upper and lower chambers is 44 and 11 liters, respectively.

Air flow system. Air was pumped through an Aadco pure air generator to remove hydrocarbons and CO_2 and reduce the dew point. Carbon dioxide and water vapor were added back to the air stream to obtain desired concentrations. Air flow into the inlet port of the gas-exchange chamber was monitored by a flow meter and ranged from 2 to 5 l/min depending on plant size and environmental conditions. Air samples for CO_2, dew point and isoprene analysis were taken from sample ports at the chamber inlet and outlet, respectively. Air temperature within the upper chamber was monitored with a shielded thermocouple and leaf temperature with a thermistor clipped to the undersurface of the leaf in the mid-canopy. Light provided by the controlled environment chamber was monitored in the upper chamber with a Lambda Instruments model LI-190SR Quantum Sensor. The dew point of the air entering the gas exchange chamber was held constant during each experimental run and was measured with a dew point hygrometer. Inlet and outlet CO_2 concentrations of the air stream ranged from 400 to 600 and 310 to 390 μl/l, respectively, and were measured with an infra-red gas analyzer. Changes in the CO_2 concentration in the chamber were not large enough to have any significant effect on isoprene emission rates (Jones and Rasmussen 1975).

Hydrocarbon sampling and analysis. Isoprene was chromatographically separated using a 3 m × 3.2 mm OD stainless steel column containing Porasil E (80/100 mesh)/Alltech CS-10 (10% stationary phase). Analyses were performed isothermally at 90°C using helium (20 cm^3/min) as a carrier gas and the isoprene was measured with a flame ionization detector. Since a flame ionization detector responds linearly to the mass organic carbon (David 1974), a 1.01 μl/l isooctane standard was used to calculate the mass of organic carbon emitted as isoprene. Three to 6 isooctane standards (1 ml) were taken daily with a reproducibility of ±2%. A 99.9% pure standard of isoprene was used to establish the isoprene retention time and profile.

Air samples (20 ml) were collected from the sample ports of the gas exchange chamber using a 100 ml gas-tight syringe. The samples were injected through a six-port valve into a stainless steel trap (61 cm × 0.25 mm ID) immersed in liquid oxygen to concentrate the hydrocarbon sample (Rasmussen *et al.* 1974). Following sample injection the stainless steel trap remained in the cryogen for a 4-min period with the helium purge flow (13 cm^3/min) through it. The concentrated sample was volatilized onto the gas chromatograph column by rapidly heating the trap in boiling water.

Positive identification of the isoprene emissions from live oak was made by a combination of gas chromatography and mass spectrometry using the same gas chromatographic operating conditions as cited above. The isoprene mass spectra were compared to the Registry of Mass Spectral

Data (Stenhagen *et al.* 1974) and a 99.9% isoprene standard to confirm identification.

Experimental protocol. The influence of temperature on isoprene emissions at various light levels was studied by increasing the leaf temperature from 20 to 47°C in 4 to 6°C increments at each of four light levels (approximately 100, 200, 400, or 800 μE m^{-2} s^{-1}). To measure the effect of light intensity on isoprene emissions, light intensity was increased stepwise 0, 100, 200, 400, and 800 μE m^{-2} s^{-1} at each of four leaf temperatures (29, 35, 41, or 47°C). After each change of light or temperature, a 60 min equilibration period was observed before collecting triplicate air samples for hydrocarbon analysis. A minimum of three plants was used to develop each temperature or light response curve. After each experiment, leaves were removed and the leaf area determined.

Data analysis. The relationship between means and standard deviations of samples taken at each light and temperature level indicated that isoprene emission rates followed the lognormal statistical distribution. Therefore, the emission data were transformed to their respective logarithms for all statistical analyses. Also the use of the logarithmic scale made it possible to fit all light and temperature data with the same mathematical function. Means of the triplicate samples collected at each light and temperature combination were computed and used to estimate the isoprene response curves.

Experimentation (*e.g.*, Sanadze and Kalandadze 1966a, Rasmussen and Jones 1973) and biological theory suggested that the isoprene response curves should approach asymptotically their maximum values. Third order polynomial, rational and logistic functions were considered as models for the response curves. The logistic function was selected because it had good asymptotic properties and best fit the data. The logistic function selected is similar to the one used to model plant growth curves except a fourth parameter (D) has been added which allows the minimum to be different from zero. The equation for the four-parameter logistic function is:

$$F(x) = \frac{A}{1 + \exp[-B(x - C)]} + D$$

A = the difference between the minimum and the maximum values of the function.

B = shape parameter which determines how quickly the function goes from its minimum to maximum.

C = location parameter which determines the point along the X axis where the curve is centered.

D = minimum value of the function.

Since the logistic function is nonlinear in its parameters, a nonlinear least squares procedure (Marquardt 1970) was used to estimate the parameters of the response curves. Means of isoprene emissions or the carbon loss/carbon gain ratio above 44°C were not used to estimate temperature response curves because the data no longer fitted the logistic curve.

Table 1. *Isoprene production* (μg C dm^{-2} h^{-1}) *under constant environmental conditions.* Plants were held at constant environmental conditions (leaf temperature, 35°C; light intensity, 400 μE m^{-2} s^{-1}); triplicate samples were collected hourly and mean emission rates determined. Hours indicate time after the lights were turned on in the controlled environment chamber.

Hours		Plant 1	Plant 2
3		32.1	—
4		43.0	37.7
5		34.5	39.3
6		34.2	39.9
7		35.3	37.1
8		38.6	38.9
9		40.3	41.1
	$\bar{x}$	36.8	39.0

Results

Initial studies were conducted to determine if isoprene emission rates remained constant over time when the environmental conditions were held constant. Emission rates were measured over a 5 to 6 h period after the plants were in the light for 3 or 4 h (Table 1). The flux estimates varied ±4 and ±2 μg C dm^{-2} h^{-1} about the means for plants 1 and 2, respectively, indicating that plants could maintain a high isoprene emission rate for extended time periods.

Increasing the light intensity significantly increased isoprene emission rates at all temperatures until maxima were reached (Figure 2). In the dark at all temperatures, isoprene emissions were low (1 μg C dm^{-2} h^{-1} or less). As light intensity increased, isoprene emissions increased significantly to about 75 μg C dm^{-2} h^{-1} at 35 and 41°C and 800 μE m^{-2} s^{-1}. At the highest light intensity (29–41°C), light saturation of the isoprene emission process was approached (within 5%) or reached. However, at 47°C increasing light elicited only a slight increase in isoprene emission.

Isoprene emission rates increased with temperature at each of the four light levels (Figure 3). The temperature-induced increases in emission rates became greater with increased light intensity. Maximum isoprene emissions occurred between 40 and 44°C with the largest emissions (about 100 μg C dm^{-2} h^{-1}) at the highest light level and 44°C. At temperatures above 44°C for all light levels, there was a sharp decline in isoprene emissions to approximately 2 to 4 μg C dm^{-2} h^{-1} or less. When the higher temperatures persisted for several hours, marginal leaf necrosis developed. No emission data were collected below 27°C at the highest light intensity because the gas-exchange chamber could not be cooled to lower temperatures under the radiant energy load.

To determine the influence of temperature on isoprene emission rates, the temperature coefficient (Q_{10}) was calculated at several light intensities (Table 2). The boiling point of isoprene is 34°C, therefore the Q_{10}'s were calculated using temperature ranges above and below that temperature.

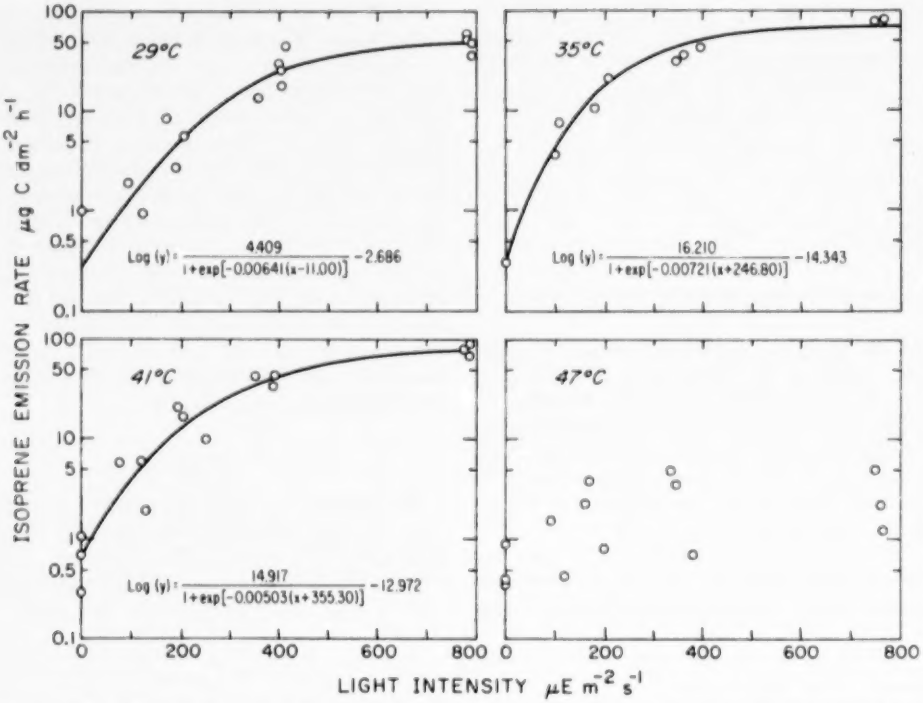

Figure 2. *Influence of light intensity on isoprene emissions from live oak at several leaf temperatures.* An equation was not fitted to data at 47°C because parameter estimation of the nonlinear equation did not converge. Each circle is a mean of triplicate observations from the same plant. The equation for each line is given.

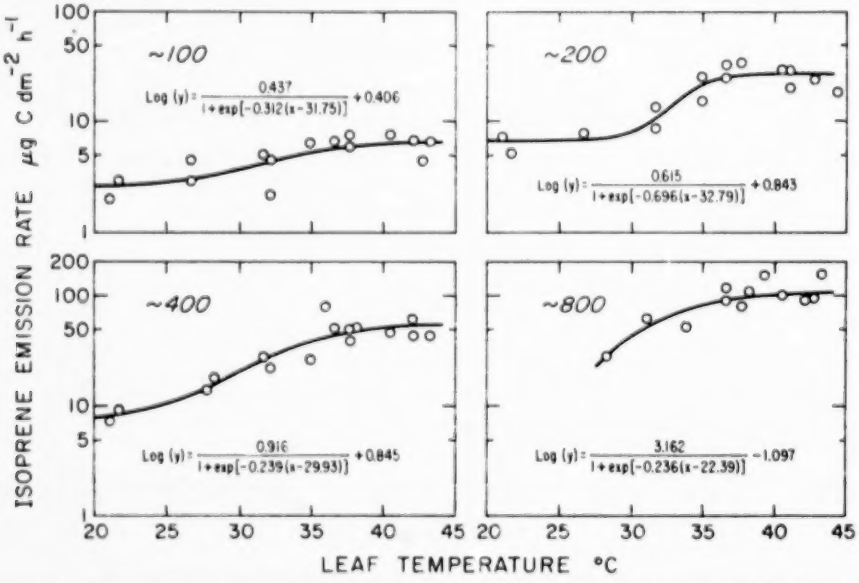

Figure 3. *Influence of leaf temperature on isoprene emissions from live oak at several light intensities.* Each circle is a mean of triplicate observations from the same plant. The equation for each line is given.

Table 2. *Temperature coefficients of isoprene production as a function of light intensity.* The Q_{10}'s were calculated using the van't Hoff equation and data from Figure 3. (†) Value derived over the temperature range of 29 to 34°C.

Light intensity $\mu E\ m^{-2}\ s^{-1}$	Temperature range for Q_{10}, °C	
	25–34	35–40
100	1.9	1.5
200	3.2	1.6
400	3.8	1.8
800	3.9†	1.6

Below 34°C, the Q_{10}'s were large and increased with light intensity from 1.9 to 3.9. But above 34°C, the Q_{10}'s were small (1.5 to 1.8) and were independent of light intensity.

To determine the relationship between isoprene emissions and net carbon dioxide fixation, concurrent measurements of emission and fixation were made for each plant. The net photosynthetic rate increased with light intensity and decreased slightly with temperature over the range studied (data not shown but can be derived from Figures 2–5). Isoprene emissions increased more rapidly with increasing light intensity than did carbon dioxide fixation as indicated by the increased ratio of carbon lost as isoprene to carbon fixed in photosynthesis (Figure 4). At temperatures below 47°C and at 100 $\mu E\ m^{-1}\ s^{-1}$ carbon lost as isoprene was approximately 0.1–0.5% of the carbon photosynthetically fixed; it increased significantly to a level about eight times as great at 41°C and 800 $\mu E\ m^{-2}\ s^{-1}$ (1–2%). However, at 47°C, the carbon loss/carbon gain ratio was low and increasing light intensity did not increase the ratio. As the light intensity increased, light saturation of the carbon loss/carbon gain ratio was approached or reached. Similarly, increases in leaf temperature at each light intensity increased the carbon loss/carbon gain ratio (Figure 5). Maximum carbon loss occurred between 40 and 44°C. The largest ratio (about 2%) occurred at the high light level and 44°C. At temperatures above 44°C for all light levels there was a sharp decline in the carbon loss/carbon gain ratio.

Discussion

The effects of light and temperature on isoprene emission rates were interdependent. The maximum emission rates (light saturated) increased with temperature up to approximately 41°C. The light saturation and light dependency of isoprene emission rates from live oak were similar to

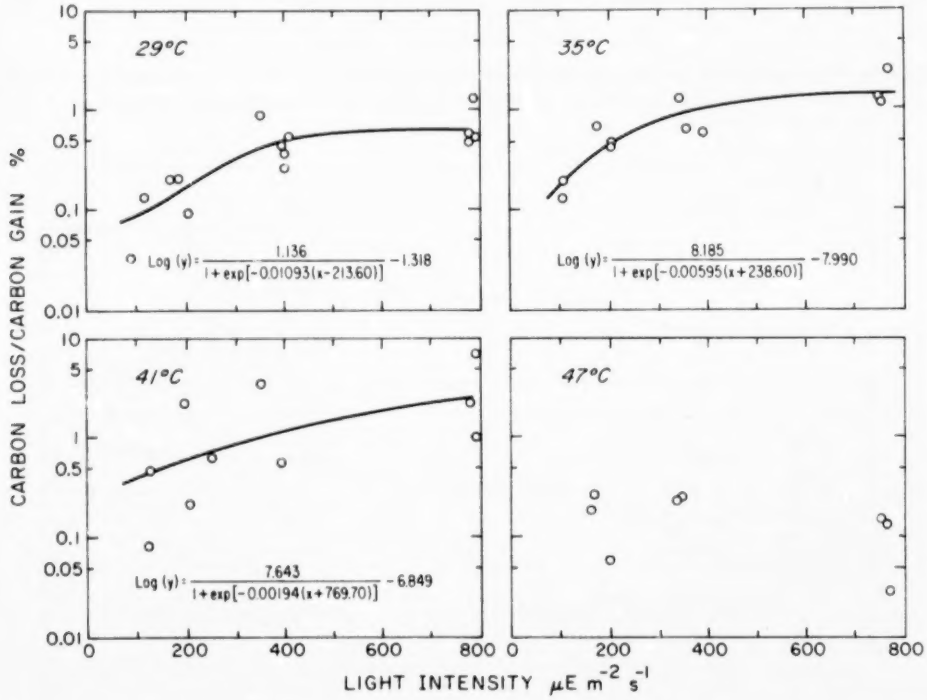

Figure 4. *The influence of light intensity on the ratio of carbon lost as isoprene to net carbon fixed in live oak at several leaf temperatures.* An equation was not fitted to the data at 47°C because parameter estimation of the nonlinear equation did not converge. Each circle is a mean of triplicate observations from the same plant. The equation for each line is given.

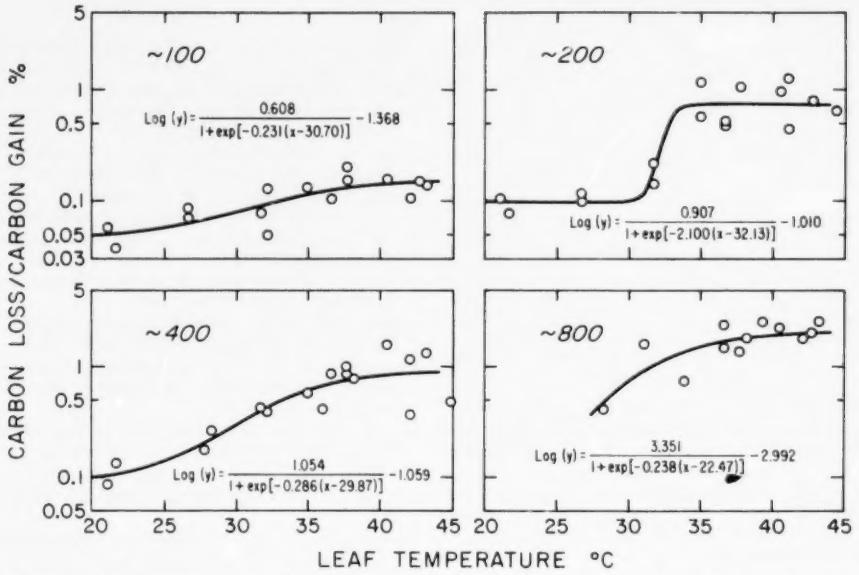

Figure 5. *The influence of leaf temperature on the ratio of carbon lost as isoprene to net carbon fixed in live oak at several leaf temperatures.* Each circle is a mean of triplicate observations from the same plant. The equation for each line is given.

responses reported for other plant species (Sanadze and Kalandadze 1966a, Rasmussen and Jones 1973). Also, increasing temperature up to 44°C caused a greater increase in emission rates at high light intensities than at low light intensities. Isoprene emission rates from live oak exhibited similar temperature stabilities (maximum emission rates between 40–44°C) as reported for other species (Sanadze and Kalandadze 1966a, Rasmussen and Jones 1973), except that higher temperature (47°C) was required to thermally decrease emissions.

The flux of a gas is proportional to the chemical potential gradient and inversely proportional to the resistance of the pathway. The chemical potential gradient that drives isoprene emissions from leaves is the isoprene vapor pressure gradient existing between the leaf interior and the ambient air. The vapor pressure of isoprene is proportional to the isoprene concentration or pool in the leaf and to leaf temperature. The primary importance of light is to provide the photochemical energy to drive isoprene biosynthesis (Sanadze and Kalandadze 1966a, Rasmussen and Jones 1973). Light could also alter the resistance of the diffusion pathway, but Jones and Rasmussen (1975) suggested that stomata did not control isoprene emission. Temperature directly influences emission rates by altering the isoprene vapor pressure which increases at the relative rate of 4.2%/°C over the ambient temperature range (Jordan 1954), equivalent to a Q_{10} of 1.52. Temperature also indirectly influences emission rates through its influence on the rate of enzymatic reactions, which can affect isoprene pool size. The magnitudes of the Q_{10}'s (1.9–3.9) indicate the enzymatic (thermochemical) nature of isoprene biosynthesis and this is supported by the data of Sanadze and Kalandadze (1966a). Based on the rate-limiting reaction concept, the Q_{10}'s can be used to determine the limiting step in a series of reactions (Giese 1973). The magnitudes of the Q_{10}'s (1.9–3.9) below the isoprene boiling point (34°C) indicate that isoprene biosynthesis or pool size is the factor controlling emissions. However, above 34°C the magnitudes of the Q_{10}'s (1.5–1.8) suggest that isoprene emission rate is controlled primarily by diffusion.

Isoprene emissions by oak plants represent a significant loss of photosynthetically fixed carbon, approximately 0.1 to 2%, depending on light intensity and temperature. Sanadze (1969) reported that *Populus nigra* lost 1% of its photosynthetically fixed carbon as isoprene at 30°C and moderate light intensity; this is similar to the amount lost by live oak at that temperature. The carbon loss rate as isoprene is significantly larger than the 0.06% carbon loss as monoterpenes from Salvia (Tyson *et al.* 1974). The greater carbon loss as isoprene probably occurs because it has a higher vapor pressure than monoterpenes.

To illustrate the interaction of light and temperature on isoprene emissions, typical diurnal isoprene emission patterns were derived. The environmental conditions for an average of summer days in Tampa, Florida and the estimated isoprene emission rates interpolated from the light intensity and temperature response curves (Figures 2 and 3) were used in the derivations. Climatic summaries (*e.g.*, Visher 1954, NOAA 1974) indicate an average daily solar radiation of approximately 2.1 $kJ \cdot cm^{-2}$ and average maximum and minimum air temperatures of 32 and 20°C, respectively during the summer. The hourly values for solar

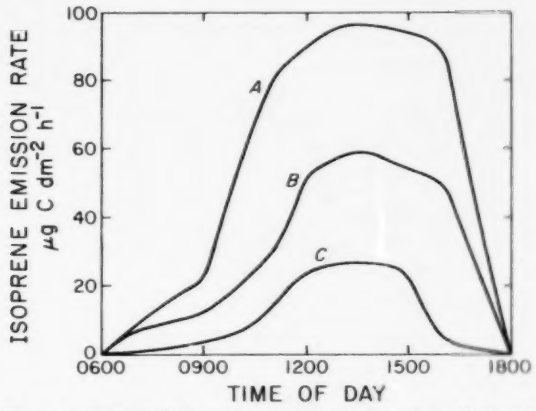

Figure 6. *Estimated isoprene emission rates from live oak trees in Tampa, Florida for an average of summer days.* A — sunlit leaves (assumed leaves hotter than air temperature); B — shaded leaves (assumed leaves 1 °C less than air temperature and radiation intensity equal to 1/2 ambient sunlight); C — shaded leaves (assumed leaves 1 °C less than air temperature and radiation intensity equal to 1/4 ambient sunlight). 800 μE m^{-2} s^{-1} equals approximately 2.1 J · cm^{-2} · min^{-1}.

radiation flux were estimated by assuming that the flux varied sinusoidally with a maximum (4.6 J · cm^{-2} · min^{-1}) at local noon and 0 at 0600 and 1800 h, respectively. The average hourly air temperature was inferred from the observed maximum and minimum temperatures and what was known about typical diurnal temperature cycles. Empirical results from our laboratory indicated that the temperature of sunlit leaves was related to the air temperature by the following equation: $T_l = 1.25\ (T_a + 0.9)$, where T_l is leaf temperature and T_a is air temperature. The leaf temperature for shaded leaves was assumed to be 1 °C less than air temperature. Estimated hourly emission rates of isoprene from live oak trees in the vicinity of Tampa, Florida are shown in Figure 6. As expected, the predicted maximum emission rates occur during midday. During early morning and late afternoon hours when temperatures are moderate and leaves are not light saturated, light is the main factor controlling emission rates. However, during most of the day, the leaves of the outer canopy are light saturated (curves A and B) and varying air temperature controls the emission rates. In contrast, for heavily shaded leaves (Curve C), not light saturated, the light intensity is important throughout the day. More than 80% of the daily isoprene emissions from oak trees is expected to occur after 1000 h. The isoprene emission rates estimated from the model and reported in Figures 2 and 3 were similar to emission rates reported for oak in the Tampa, Florida area (P. R. Zimmerman, unpublished).

Edited by A.K.

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